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THE GENERAL MORPHOLOGY OF THE FEMALE REPRODUCTIVE SYSTEM OF A VIVIPAROUS ROACH, *DIPLOPTERA DYTISCOIDES* (SERVILLE)

By Harold R. Hagan

College of the City of New York

This widely distributed roach is rather robust and broad yet only three-fourths of an inch in length. It was collected by the author and an assistant, Mr. Francis Yap, some years ago in the Hawaiian Islands. This work on it was undertaken only last summer at the Biological Laboratories, Harvard University, where facilities were provided through the courtesy of Professors C. T. Brues, A. B. Dawson and Leigh Hoadley. Acknowledgement should likewise be made for the results obtained by my colleague, Professor James I. Kendall, in photographing sections not especially favorable for photomicrographs.

The method of reproduction by this roach made an examination of the genital tract eventually inevitable though only its general conformation will be given here. Fortunately, Snodgrass (1933) has rendered the task much easier by his excellent illustrations and detailed description of these parts in *Blatta orientalis*. The reproductive systems of the two species possess similar subdivisions varying only in their shapes, relative sizes and functions. To reveal these homologies, the reproductive system of *B. orientalis* has been shown in figure 1. It will at once be seen that the vestibule has been shortened in the viviparous species to be described while, on the other hand, *orientalis* possesses the rudiments

of a genital pouch above and a brood sac below the junction of the oviduct with the genital chamber. These rudiments may have no important specific function in this species for, it will be recalled, the female is oviparous and utilizes the vestibular portion of the genital chamber for oöthecal formation and placement of the eggs within the oötheca cast there. Figure 2 gives diagrammatic dorsal and lateral views of this system in *D. dytiscoides*. The brood sac is somewhat enlarged and asymmetrical in shape for eggs with young embryos are enclosed. They are placed diagonally because their slightly narrower micropylar ends, occupying less space, are directed toward the left.

Six ovarioles comprise an ovary which is cone-shaped with the base resting on the distal end of a paired oviduct. Each ovariole tapers anteriorly to the germarium and terminal filament in the usual fashion. The former contains twenty or thirty oögonia within its lumen and there are always seven or eight clearly discernible oöcytes within the vitellarium or lower portion of the ovariole; two more than shown in the upper ovariole in the figure, for only part of the

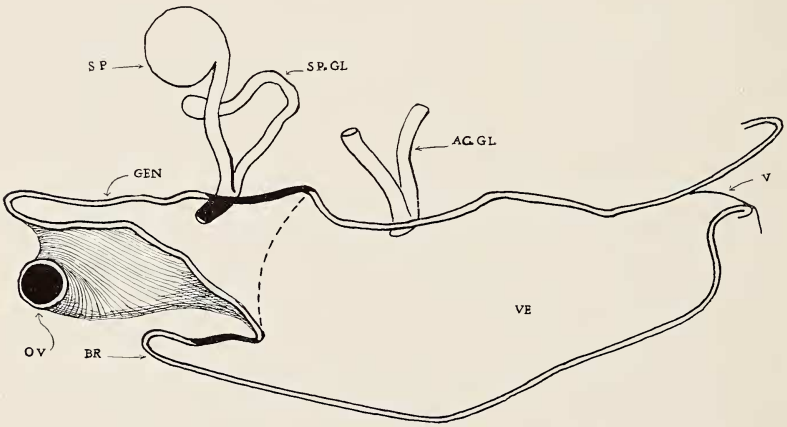


Figure 1. *Blatta orientalis*. Diagrammatic median section through the genital chamber of the female reproductive system. AC.GL, accessory gland; BR, rudiment of a brood sac; GEN., rudiment of a genital pouch; OV, cross-section of proximal end of left oviduct; SP, spermatheca; SP.GL, spermathecal gland; V, vulva; VE, vestibule. (Redrawn and relabelled from Snodgrass, 1933: Smithsonian Miscellaneous Collections, v. 89, no. 8)

seventh is visible at the left. Their panoistic arrangement and structure are typical of roaches.

The paired oviducts are short, stout tubes which convey the oöcytes from the ovaries. Each bears a slightly dilated distal end which might be termed the calyx of the oviduct. From the latter arise six terminal or subterminal urn-shaped pedicels. The lumen of the pedicel is continuous with that

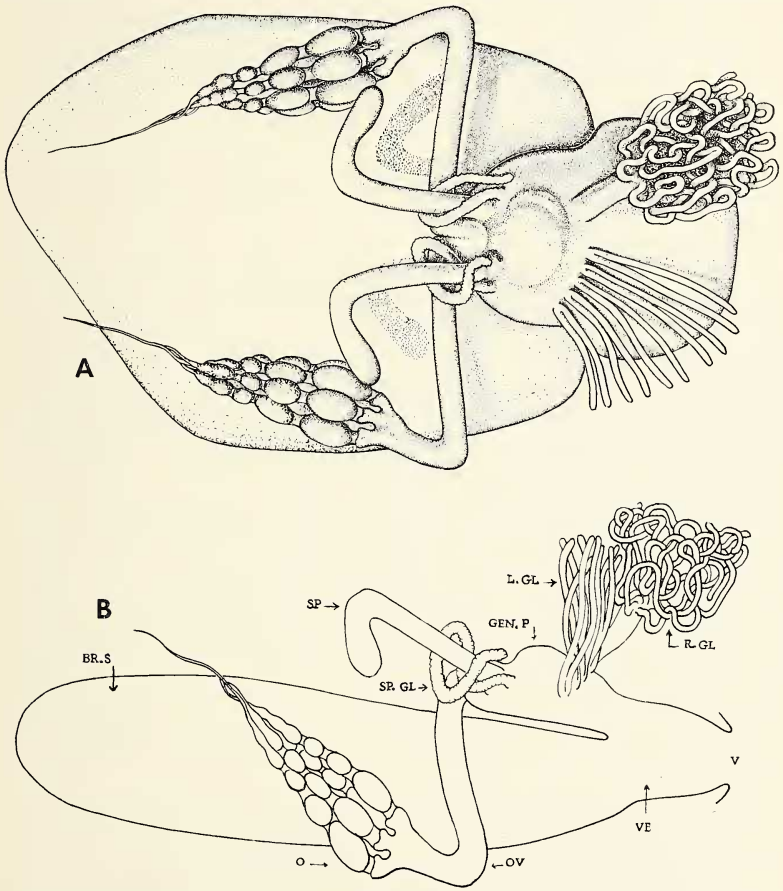


Figure 2. *Diploptera dytiscoides.* Diagrammatic views of the female reproductive system. A, dorsal aspect above; B, lateral aspect below. BR.S, brood sac; GEN.P, genital pouch; L.GL, left accessory gland; O, ovary; OV, oviduct; R.GL, right accessory gland; SP, spermatheca; SP.GL, spermathecal gland; V, vulva; VE, vestibule.

of the calyx but distally it ends blindly. The proximal end of an ovariole joins the blind end of each pedicel.

The wall of the paired oviduct is muscular while its lumen is lined by an epithelium which may be thrown into deep folds when it contains no oöcyte. Each oviduct extends a short distance ventrally and posteriorly, then bends abruptly toward the midline of the body. As the two meet each turns sharply posteriorly. At this point they are enclosed in a common peritoneum and musculature but their lumens are quite independent. This condition is illustrated by Plate 1, fig. 4 which also shows the epithelial folds previously mentioned. The united oviducts discharge almost immediately into the median oviduct. The latter is much abbreviated, lies within the wall of the atrium and differs from a paired oviduct only in the possession of a smooth, fairly thick, internal cuticula.

The genital chamber, or vagina as it is frequently termed, continues the tract to its external opening. It is by far the largest part of the reproductive system and the most interesting to the student of viviparity. The illustrations show it to be divided into a genital pouch or atrium, a brood sac or uterus and a vestibule. All bear a heavy musculature, but that of the uterine portion is much greater for from this chamber parturition takes place.

The genital pouch has a flat floor whose cuticula is irregularly folded over its posterior half. At the proximal margin it bends downward and becomes continuous with the roof of the underlying uterus. Its roof bears a slight elevation where the median oviduct joins it anteriorly, and a more pronounced central dome which, no doubt, facilitates the tilting of the eggs as they pass into the uterus. From its dorsal surface, too, various glands and the spermathecæ project into the body cavity. They will be discussed presently.

Considerable activity is centered in the genital pouch. In it the oöcytes are inseminated, directed into the brood sac and provided with an oötheca. These activities are coordinated by the operation of the valves of the ovipositor which lie in its lumen. In addition, the spermatophores from the male are deposited here till further disposition is made of their essential elements.

The uterine portion is huge compared with the rest of the tract and is capable of enormous distention during gestation. Plate 1, fig. 2 is particularly striking since fourteen developing eggs may be seen in it, while twelve is the usual number. The arrows point to two embyros which will not survive for they are forming in immature oöcytes. An empty uterus is always much folded and its cuticula and epithelium are thrown into massive fungiform papillæ. The vestibule is short, connecting with both atrium and uterus anteriorly and opening to the outside of the body by means of the posteriorly situated vulva. It is quite muscular and the intima is beset with low conical papillæ, each bearing a delicate seta.

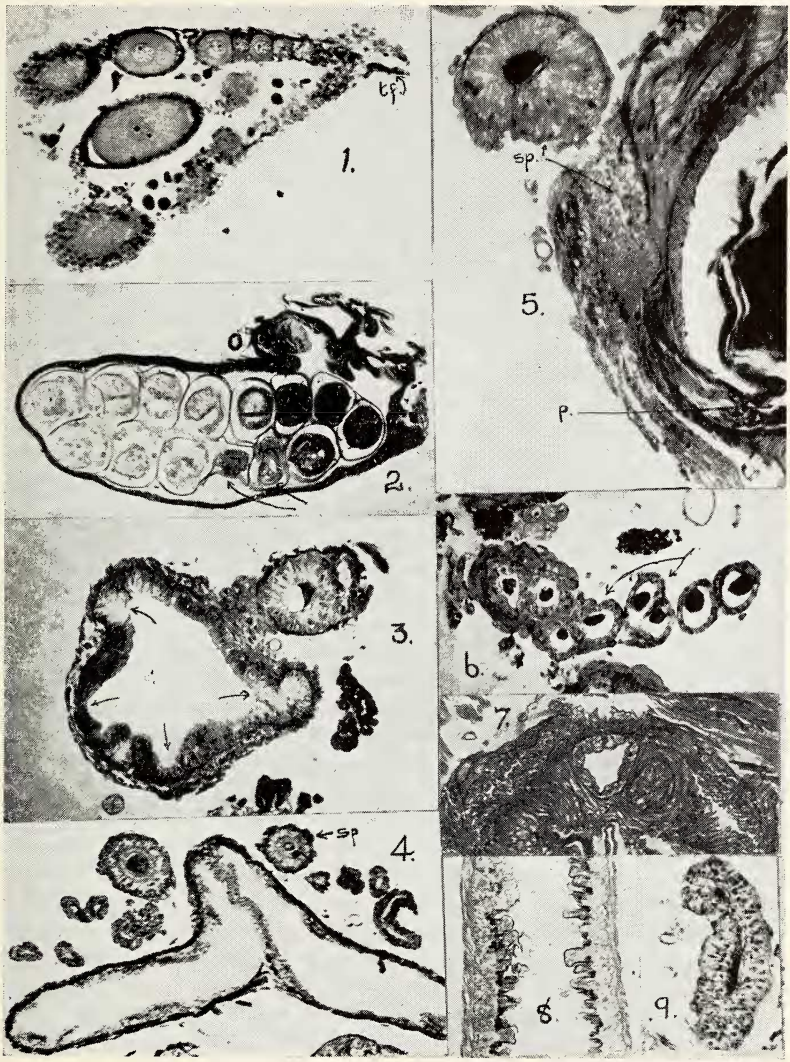
The spermathecæ are two simple, tubular glands. Each projects into the body cavity from the roof of the genital pouch on either side of the elevation formed by the insertion of the oviduct. Their muscular walls enclose a remarkably tall, columnar epithelium with a cuticula bordering the relatively narrow lumen. The spermatozoa are bent in an arc at right angles to the length of the organ, hence the oldest gametes must be situated farthest from the opening in the atrium. The proximal ends of the spermathecæ traverse the distal wall of the latter and open from papillæ above the gonopore. A laterally placed spermathecal gland entwines each spermatheca and accompanies it through the atrial wall. This gland possesses an irregular superficial outline, thick walls and a narrow lumen. The latter is constantly filled with an intensely basophilic secretion.

Posterior to the median dome in the roof of the genital pouch lie two large glands. The left one is termed a crystalloid gland for its lumen always seems to contain granular secretions. Perhaps it, too, contains the proteinaceous basal substances which form the oötheca and thus conforms to the glands studied by Bordas (1909), Ito (1924), Pyror (1940) and others. Because of its persistent secretory activity, however, it may be a nutrient organ for the embryos. Its duct, upon leaving the lumen of the atrium, widens into an ampulla or reservoir, narrows quickly again, then branches four times toward the left to produce five tubes which reach the surface of the atrium. Just at the surface each one divides again to thrust a total of ten simple tubes

straight upward into the hæmocœlar space. The arrows indicate two steps in such a division of the ducts though only eight of the ten branches are visible in Plate 1, fig. 6. Adjacent to this gland another is found to the right of the median line. Its general course is the same in the atrium but its walls are thick and the lumen practically closed. It appears in the hæmocœle as a stout column with an open lumen terminating in a calyx. From the latter arise approximately twenty very long, narrow, simple glandular tubes which coil around one another to form a compact knot. Its function is problematical. The six valvulæ of the ovipositor are approximately uniform in length yet no longer than the largest in *B. germanica*. They are, however, narrower and more delicate organs in *D. dytiscoides* than in the latter species. Two pairs are wide basally but taper distally to smoothly rounded tips. The valvulæ of the third pair are very slender throughout their length. They are not illustrated.

This, very briefly, is an outline of the female reproductive system of *Diploptera dytiscoides*. While its component elements introduce no new structures which *B. orientalis* lacks, still some of them vary greatly from the latter species that maternal care and incubation may insure viviparity. Such changes include a reduction in the number of ovarioles with a consequent limitation of the offspring to be accommodated at any one time. The lowered reproductive rate may also be associated closely with the apparent necessity for maternal nutrition of the embryos till hatching and birth, and the possible modification of the nature of the secretion from the right gland to furnish the required amount of nutriment. The oötheca, in turn, is reduced to a thin membrane which only partially envelops the egg mass and never turns brown upon contact with the products of the right gland as Pyror states is the case in oviparous species. Finally, the uterine portion of the genital chamber is definitely established as an enormous incubatory receptacle for the embryos till hatching. The maintenance of oviparous parts and accessories in the viviparous production of offspring once more recalls the old adage that "morphology is more conservative than physiology."

PSYCHE, 1941 VOL. 48, PLATE I.



Hagan — *Diploptera dytiscoides*